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The Utility of the Proximate-Ultimate Dichotomy in Ethology

JOHN ALCOCK & PAUL SHERMAN

ALCOCK, J. & SHERMAN, P. 1994: The utility of the proximate-ultimate dichotomy in ethology. *Ethology* 96, 58—62.

Abstract

We defend the organizing principle that there are fundamentally different levels of analysis in biology, notably proximate and ultimate. Despite recent claims to the contrary, the proximate-ultimate distinction is a true dichotomy, not an artificial division of a continuum. Acceptance of this dichotomy does not imply that ultimate questions are of greater importance than those dealing with proximate mechanisms, nor does it result in confusion of current reproductive consequences with evolutionary causes.

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DEWSBURY (1992) recently summarized the ways biologists compartmentalize behavioral research. He argued for the abandonment of the most widely used organizing system, namely the one in which questions and hypotheses are labelled as either proximate (dealing with immediate causes, the internal mechanisms and development of behavior) or ultimate (dealing with evolutionary causes, the history and reproductive consequences of behavior). In its place, DEWSBURY offered a three-part organizational scheme in which questions and hypotheses are categorized as dealing with either the genesis, control, or consequences of behavior.

In defending his new system DEWSBURY made a number of critical statements about the proximate-ultimate dichotomy that we feel merit reconsideration. The first of these is that (p. 98) "... in the study of animal behavior ... all

distinctions that are initially proposed as dichotomies are destined to become continua." We disagree. The vast majority of behavioral hypotheses and questions can be assigned unambiguously to either the proximate or ultimate category.

In identifying supposed ambiguous cases, DEWSBURY pointed to (1) cultural inheritance as an explanation for human behavior, and (2) several physiological and phylogenetic constraints on evolution. With respect to (1), whatever "problem" of assignment that exists arises because there can be two general versions of the cultural inheritance hypothesis. It is a proximate hypothesis when an individual's behavior is being explained in terms of the learned cultural influences that affected his/her ontogeny, but it is an ultimate hypothesis when an individual's behavior is being explained in terms of the history of the culture to which the individual belongs. The ultimate version of the hypothesis is often based on a theory of cultural selection (e.g., BOYD & RICHERSON 1985), rather than Darwinian natural selection of alternative alleles. It assumes that the history of any culture was characterized by competition between alternative culturally transmitted behavior patterns, a competition that influenced what learning experiences are available to shape the development of an individual's behavior.

Similarly, there is no ambiguity in assigning constraints hypotheses to the ultimate column when such hypotheses are designed to explain, as they typically are, why animals have evolved certain attributes. The usual constraints hypothesis (e.g., WAKE 1991; ARNOLD 1992) deals specifically with evolutionary forces other than natural selection that might affect the historical pathway leading to a currently existing trait. The fact that these other forces include physiological, genetic, and developmental proximate mechanisms which are widespread within a species will not cause confusion if it is clear that the goal of the hypothesis is to explain evolutionary history.

Thus, DEWSBURY did not provide any convincing examples in which proximate and ultimate questions and hypotheses could not be distinguished. This lack of evidence also undercuts DEWSBURY's second criticism, namely that attempts to use the proximate-ultimate dichotomy have obfuscated certain issues in behavioral biology. Here the key example DEWSBURY offers is the controversy over the adaptive significance of the human clitoris and female orgasm (GOULD 1987a, b vs. ALCOCK 1987; JAMIESON 1989 vs. SHERMAN 1989).

Contrary to DEWSBURY, the clitoris debate did not arise because of failed efforts to fit competing explanations into the proximate-ultimate mold. All the protagonists offered ultimate hypotheses, but as MITCHELL (1992) pointed out, their explanations fell into two groups: those proposing that clitorises and orgasms currently contribute to female reproductive success as the probable outcome of past episodes of natural selection *versus* those proposing that clitorises and orgasms have no effect on female fitness, but are maintained as a nonadaptive, pleiotropic effect of an adaptive developmental system of mammalian sexual differentiation. The controversy thus stems from semantic arguments over how to define adaptation (see REEVE & SHERMAN 1993) and the difficulty of devising definitive tests for the competing hypotheses, rather than from any failure of the proximate-ultimate dichotomy to accommodate the debate.

Semantic issues also underlie another of DEWSBURY's criticisms, namely the supposed confusion of consequence with cause by persons engaged in ultimate analyses. DEWSBURY claimed, as have others (e.g., SYMONS 1990; FRANCIS 1990; ARMSTRONG 1991), that explanations of a behavior based on its present consequences for survival and reproduction mix up current fitness effects with past causes, despite the undeniable point that "events cannot cause events that precede them" (DEWSBURY, p. 97).

Implicit in DEWSBURY's argument is the belief that adaptations are characters which evolved in the past due to natural selection. Most persons who explore the adaptive value of traits, however, attempt to determine how they currently affect reproductive success. Such persons define an adaptation as a trait that confers the highest fitness relative to alternative phenotypes at a particular period in time (usually the present, given the practical difficulties of studying the reproductive consequences of traits in the past). Traits that are adaptations in this sense are being maintained by natural selection or are spreading through populations as a result of their current effects on fitness.

Other researchers may be interested in what evolutionary forces were responsible for the spread of a trait in the past. These persons are dealing with quite a different level of ultimate analysis, one that focuses on alternative historical scenarios. One such hypothesis is that present selection pressures are the same as those that operated in the past, which were therefore responsible for the spread of the trait that appears in a modern population. Under this hypothesis, if a given trait currently exhibits higher fitness than its alternatives, it is inferred that natural selection in similar antecedent environments probably caused the trait's initial spread.

Persons who adopt this hypothesis are not confusing consequences with causes by explaining the existence of a current trait as being due to its present effects on fitness, but rather are assuming continuity in selection over time. We believe, as apparently do most other behavioral ecologists, that this assumption is a justifiable and parsimonious foundation for proposing hypotheses about how a trait achieved predominance. DEWSBURY himself appears to have accepted the continuity assumption in developing his own organizational scheme (his Table 3); indeed he stated (p. 101) that "The loop from consequences for differential reproduction to evolution completes a circle and renders this a somewhat complete system."

Lastly, DEWSBURY (p. 97) claimed that "the proximate-ultimate distinction . . . is fraught with hidden traps. The main one lies in the surplus meaning carried by the term 'ultimate' . . . it is easy to slip from the meaning of 'ultimate' as 'distal' to that of 'more fundamental'." DEWSBURY implied that proponents of the dichotomy ignore the importance of integrating proximate and ultimate approaches for a full understanding of behavior, and championed his new three-part organizational scheme (p. 101) "as a return to TINBERGEN's (1963) system in which all problems in the study of behavior were valued equally, in contrast to recent systems in which the ultimate has been valued more than the proximate."

Again, we take exception. From MAYR (1961) and ORIANS (1962) onward, users of the proximate-ultimate distinction have explicitly and emphatically noted

the complementary nature of proximate and ultimate research. Indeed, persons who believe that the levels of analysis approach offers a useful way to conceptualize behavioral questions have gone out of their way to stress that hypotheses at one level are not inherently superior to those at another. SHERMAN (1988, p. 616), for example, wrote, "This means that there are multiple types of 'correct' answers to any question about causality. Which category of answer is more satisfactory or interesting is a matter of training and taste . . ."

We agree with DEWSBURY that "ultimate" and "proximate" have connotations that might mislead an unwary nonscientist. The same can be said for most scientific jargon (e.g., "slave making ants," "harem polygyny," "nepotism," and "levels of analysis"). The problem might be circumvented by coining entirely new words, but this tactic has its own difficulties. The general solution that enables one to use ordinary words for special scientific purposes is to make certain that others understand the particular definition that is intended for the word in its scientific context. Once someone understands the meaning of proximate and ultimate as defined by MAYR (1961), we cannot imagine how anyone could defend the view that ultimate research was somehow superior to proximate research. We know of no published examples of attempts to do so, and none was presented by DEWSBURY.

As SHERMAN (1988) noted, researchers differ in the kind of scientific study that most appeals to them. Some persons derive satisfaction from teasing apart the genetic, neuronal, developmental, or cognitive proximate mechanisms that enable an animal to carry out a particular response. Others of an ultimate bent prefer to investigate the evolutionary history of the mechanism or the current selective consequences of the behavior the mechanism controls. Some individuals are afflicted by the kind of research chauvinism that leads them to think that whatever they are interested in must be the most important of all topics. But this attitude does not result from recognizing that proximate causes differ from ultimate ones, or that there are different levels of analysis within each category. Moreover, the idea that all researchers should integrate multiple levels of analysis is both impractical and unnecessary, provided that there is open communication between workers. We believe there is a general awareness that it is helpful to use evolutionary theory to inform proximate research, just as it can be productive to use knowledge about internal mechanisms and ontogenies to raise interesting ultimate questions (see HUNTINGFORD 1993).

The whole point of making the proximate-ultimate distinction was (MAYR 1961, 1982; ORIANI 1962; LEHRMAN 1970) and still is (KOENIG & MUMME 1990; CUMMINS & REMSEN 1992) pertinent, namely to eliminate the senseless arguments that arise from confusing these two logically distinct levels of analysis. In this light, we note one of the potential problems that could arise from DEWSBURY'S new organizational system (his Table 3): some users will be tempted to set evolutionary (ultimate) and developmental (proximate) hypotheses against one another when, for example, dealing with questions of "genesis." With a realization of what is proximate and what is ultimate comes the knowledge that these types of questions and hypotheses can be complementary, rather than mutually exclusive, leading to a full and complete picture of biological phenomena. In our

opinion, therefore, it would be imprudent to abandon the concept that there are two basic categories of questions that behavioral biologists can explore and attempt to answer.

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